ACTA BIOLOGICA SZEGED, 24 (1–4), pp. 59—88 (1978)

LIGHT- AND ELECTRON-MICROSCOPIC INVESTIGATIONS INTO THE CEROMA OF DUCKS WITH PARTICULAR REGARD TO THE HERBST CORPUSCLES

A. ÁBRAHÁM

Department of Zoology, Attila József University, Szeged

(Received June 15, 1977)

Abstract

The ceroma consists of two layers, the external epidermis, and the internal corium. The epidermis is a stratified epithelium while the corium consists of connective tissue. The corium contains frequent mastocytes and there are several Schwanns' cells, Grandry and Herbst corpuscles.

In the Herbst corpuscle, three parts can be distinguished, the inner bulb, the inner cavity and the external capsule. The inner bulb consists of two cell layers each containing 8 to 10 cells. From cells 20 to 50 laminar processes come. The laminar system of any cell is connected with that of the cells before and after it, as well as with the similar system of the row on the other side.

In the axon running between the cell rows there are groups of mitochondria, dense core vesicles, clear vesicles, and neurotubuli. The axolemma is separated from the cytolemma by an easily discernible void gap. There is no synaptic organization along the membranes. The form of connection is a parallel contact.

The inner cavity consists of lamellae, bordered by fluidfilled cavities. The lamellae vary in shape and size and are characterized by long ribosome rows.

The extennal capsule consists of parallel lamellae, separated from each other by collagenous fibril bundles. The cytoplasm of the lamellae is sponge-like with, frequent oviform cistern.

Introduction

The structure and function of the afferent synapses have always particularly engaged the attention of those interested in the structure and function of the nervous system. As formations, resp. structures that inform the organism of the environment (peristasis) and its influence exerted upon the animal life, at first the epithelia came to the fore that entered into the service of the higher sensations by getting into a close contact with the nervous system in the organs of vision, audition, smelling and gustation. These were followed by those specialized in taking up mechanical stimuli, by getting into inner connection with the single nerve fibres. The possibilities for sensation grew more and more intensive and specialized when larger cell groups entered into communication by rising bundles of nerve fibres (Eimer's organ). A separate group is formed by the specialized epithelia that, jointly and severally each organized a nerve fibre connected to its terminal sector (Merkel's cell). The synaptic organs (Vater-Pacini, Herbst and Grandry corpuscles) developed as higher forms of accomodation. In these, connective-tissue sensory cells came into synaptic connection with sensory nerve fibres, developing around themselves laminar systems for increasing and ensuring the work of transferring the stimuli.

Materials and Methods

Our investigations were carried out on the piece of skin, the cere (ceroma) covering the maxilla of the domestic duck *(Anas boschas domestica)* and mallard *(Anas platyrhyncha)*. For the light-microscopic examinations there were used partly sections embedded in paraffin, and stained with haematein and eosin, partly frozen sections impregnated according to BIELSCHOWSKY—ÁBRAHÁM. The latter process proved to be very suitable for visualising the neural elements.

For electron-microscopic investigations, small pieces of ceroma were fixed in 0.5 p.c. osmic acid after being pre-fixed with glutaraldehyde. They were then dehydrated in the usual way and embedded in araldite. Sections were cut using a L.K.B. ultramicrotome and examined in a Jeol B.100 electron microscope. The investigations were performed in the electron-microscope laboratory in the Biophysics Institute of the Biological Research Centre of The Hungarian Academy of Sciences in Szeged. In the course of our work we were aided by Dr. FERENC JOÓ, leader of the laboratory, and Dr. IDA TÓTH and I should like to express my sincere appreciation to both of them.

Epidermis

The ceroma, as a typical vertebrate integument, consists of two parts. The external part is the epidermis, and the internal part, which is closely connected to it, is the corium. The epidermis is a stratified laminated epithelium, consisting of a deep inner layer *(stratum profundum)* resting on the corium, and a horny outer layer (stratum corneum). The deep layer consists of several cell rows. The upper of which is the granulous layer *(stratum granulosum)*. This is followed by the spinous layer *(stratum spinosum)* and then by the basic layer *(stratum basale)*. The cells of the granulous layer are full of round granules. Between cells, the intercellular ducts are obvious. The cells of the spinous layer are connected by the different protoplasmic processes and longer or shorter desmosomes. The nucleus is elongated, and segmented all round. The cells of the basic layer are partly elongated, and partly polyhedric. Between the cells, there are broad intercellular ducts, and the desmosomes are apparent. In the cytoplasm, the broad cisternae of the endoplasmatic reticulum are conspicoous, as well as canals and vesicles of the Golgi complexes. In addition to these, various vesicles appear in masses, or in a dispersed state. Ribosomes are arranged in rows along the cisternae of the endoplasmic reticulum, but there are also some free groups. In the horny layer *(stratum corneum)*, layers of flat, cornuous cells are arranged one above the other. The cells consist mostly of horny threads and a nucleus is rarely seen. The desmosomes are obvious. The horny layer, and the lower layers, contain much fat. During the treatment the fat is dissolved leaving round or elliptical cavities, arranged in a line or dispersed, full of fat *intra vitam*. This yellowish mass of fat gave this piece of skin the name cere *(ceroma)* (Fig. 1).

Corium

The corium consists of two layer. One of these is a loose layer *(stratum laxum corii)*, connected with the epidermis, while the other is a compact layer *(stratum compactum corii)*. The loose layer is comparatively thin and is composed of collagenous fibrils running undulately. It contains several connective-tissue cells. The cells are long tapering into long processes at each end. The nucleus is square and the chromatin consists of compact knots. This layer has no particular characteristic features. The compact layer is thicker, consisting mostly of collagenous fibres, and contains many connective-tissue cells, Schwann's cells, and nerve fibres. The connective-tissue cells are large and have processes. In their cytoplasm there are several Golgi comp-

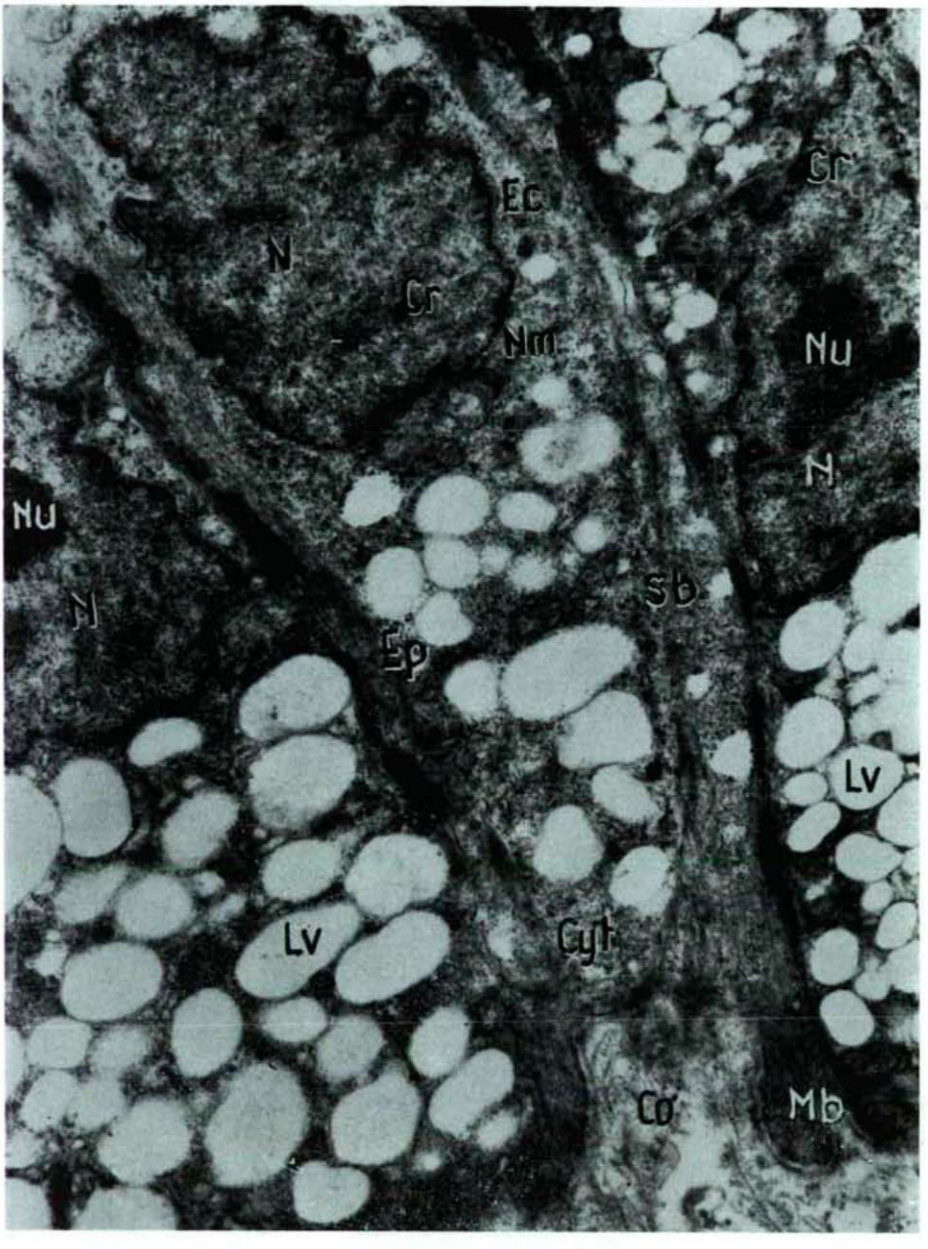

Fig. 1. Domestic duck *(Anas boschas domestica)* Ceroma. Ep = epidermis, Co = corium, Sb = stratum basale, Ec = epithelial cell, Cyt = cytoplasm, N = nucleus, Nu = nucleolus, Nm = nuclear membrane, Cr = chromatin, Lv = lipid-vesicle, Mb = membrana basalis. x16,000

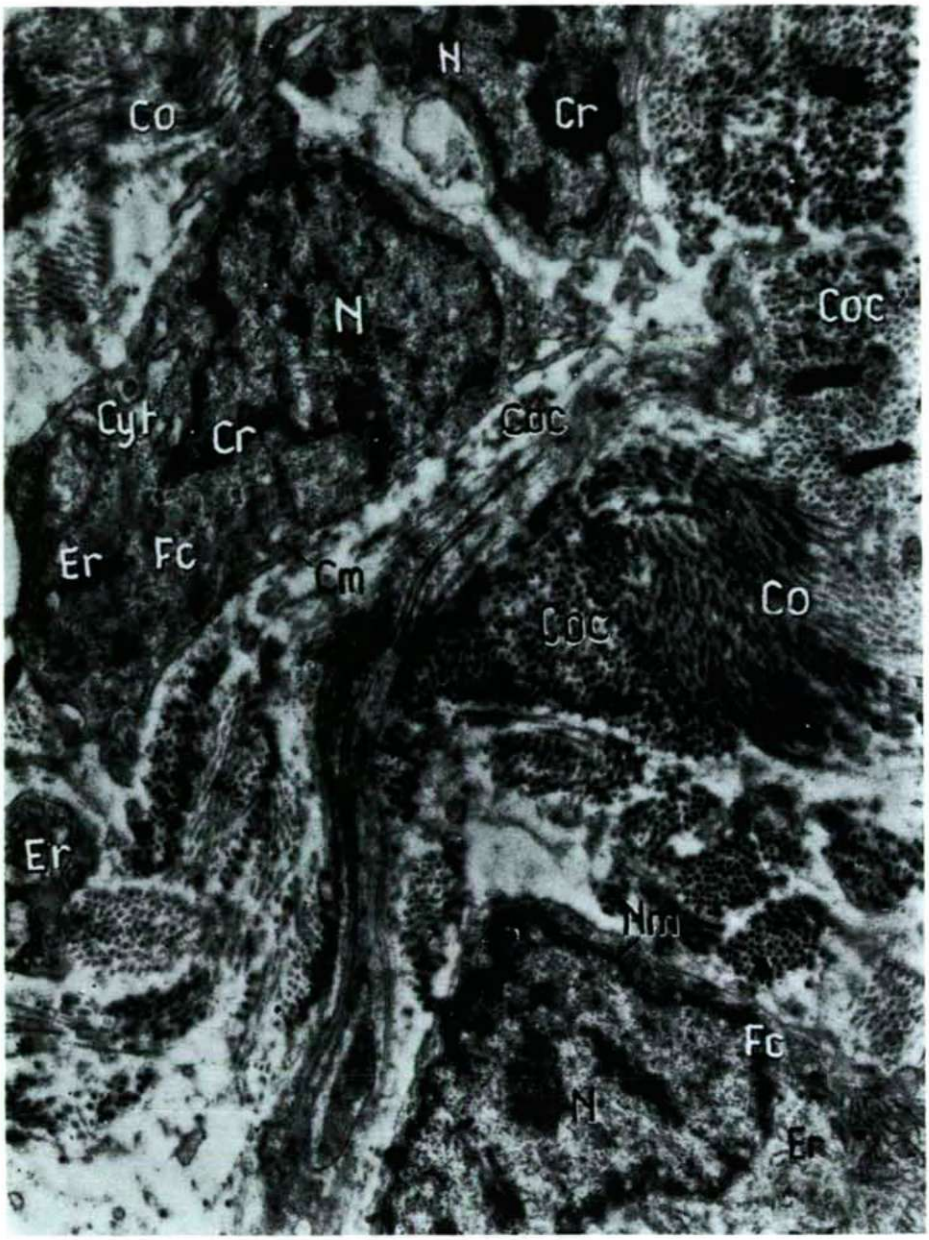

Fig. 2. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii*. Fc = fibrous-tissue cell, Cyt = cytoplasm, Cm = cell membrane, Nm = nuclear membrane, Cr = chromatin, Er = endoplasmic reticulum, Co = collagenous fibre in longitudinal section, Coc = collagenous fibre in cross-section. x16,500

lexes. The cisternae of the endoplasmic reticulum are broad. The shape of nuclei is highly variable. They may be segmented or polyhedric, and the square forms are also found. The chromatin is compact, and is concentrated directly below the membrane. A doubled membrane appears only rarely (Fig. 2).

Mastocytes

Mastocytes are rather frequent and are sharply discernible. They are not large, but elongated, sometimes segmented, cells. Their nucleus is round and contains knotty chromatin. The doubling of the membrane is obvious. The space between the two membranes is considerable, and occasionally widens out. The cytoplasm is full of round black-stained granules most of which there are empty homogeneous areas, of various sizes. Among the granules there are some which are full of smaller, uniform roundish granules. There are frequently some granule forms in the process of being discharged from granules, and others from which the contents have been fully discharged, transforming them into pale granules. These empty cells are generally named honeycomb (Fig. 3).

The most important characteristic of mastocytes, being studied by many people all over the world, is that, if excited, they discharge their metachromatic granules into the host tissue, the connective tissue (HIGGINBOTHOM, 1966). Some of the granules are taken up by the fibroblasts, but most of them go through a sudden lysis, losing histamine, their effective constituent. The mastocyte, which is an example of sequential exocytosis, resupplies its discharging granules. This has been verified experimentally (RÖHLICH, ANDERSON, UVNÄS, 1971).

In the metachromatic granules there is, in fact, an energy-demanding specific enzymatic mechanism (HÖGBERG, UVNÄS, 1957; UVNÄS and THON, 1961). This allowns the transport through the cell membrane of substances which can dissolve the biogenous amines of cells. Mastocytes are able to store, dissolve, and rebind the biogenous amines (RILEY, 1955). The process is cyclic, and has already begun in the embryo. "The ability of mast cells to discharge their metachromatic granules is their most striking histo-physiological feature and, presumably, the very basis of their biologic activity" (SELYE, 1965). It is generally supposed that the process resulting in the discharge of granules and the release of histamine, is a physiological mechanism, a response to the blood-supply requirements of tissues.

The granules of mastocytes were connected by some researchers (RHEINDORF, 1905; MEIROWSKY, 1908; JACOBI, 1912) with the granules of pigment cells. The electron microscope has provided a greater possibility to distinguish between the origin and development of these two kinds of granules. There are, nevertheless, some researchers even today who take a stand in favour of the common origin "the existence of common stem-cell". It is much more probable, however and is supported by electron-microscopic investigations, that the development of the two kinds of cells, and thus also of granules, occured in separate ways. This is also verified by the fact that we could not find any pigment cells in the ceroma of the domestic duck.

Mastocytes have been found in the various histological layers of the intestinal canal, in the respiratory tract, the serous membranes, and the lymph nodes (LEAHN, 1972). There are a great number of mastocytes in the corium, mainly in the vicinity of blood vessels, and often in close proximity to them. Some workers (ADAMS-RAY, 1959; ORFANOS, 1965; SZEKERES, 1974) found that mastocytes, and most likely the granules discharging from them are in close connection with the nerve fibres.

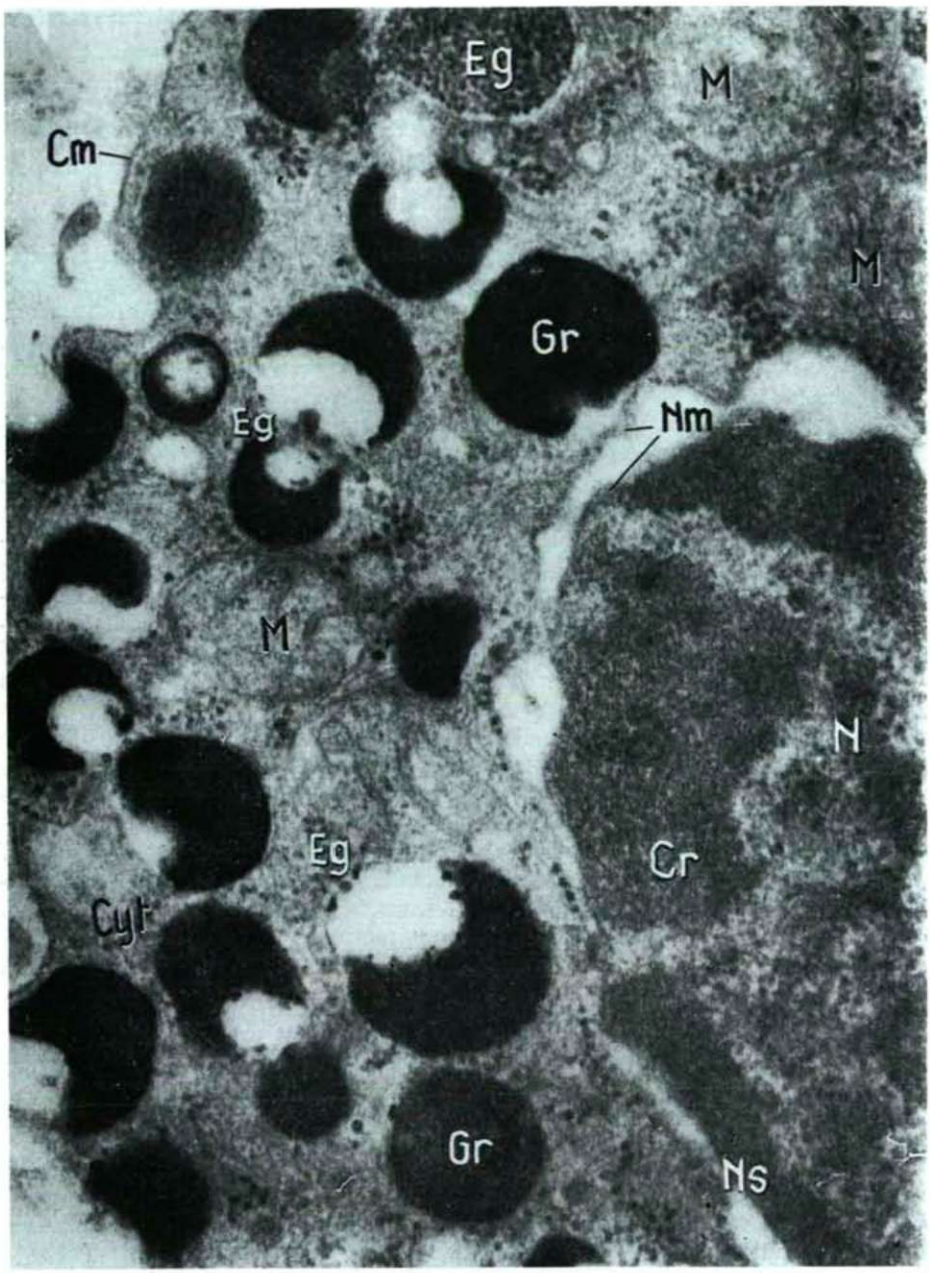

Fig. 3. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Mast cell. Cyt = cytoplasm, Gr = metachromatic granule, Eg = evacuating granule, N = nucleus, Nm = nuclear membrane, Ns = nuclear space, Cr = chromatin, Gm = cell membrane, M = mitochondrium. x260,000

Blood vessels

The capillaries are tubules of very narrow lumen. The lumen is fully filled with a single, nucleated erythrocyte. The endothelial cells are largely round with ovoid nuclei. Polymorphous nodules are formed by part of the chromatin. The erythrocytes are elongated elliptical corpuscles, strongly deformed, in the lumen of capillaries. The cytoplasm is strongly granular. Chromatin occurs along the nuclear membrane, in the form of a narrow stripe, in which broad nodules stretch towards the central part.

The postcapillary veins are tubules of characteristic structure. They appear in the microscopic pictures comparatively rarely. They are similar to capillaries but the lumen is wider and the endothelial cells are surrounded by pericytes. The endothelial cells are large and full of pinocytotic vesicles. Their nucleus is somewhat elongated but is, in fact, polymorphous. Between tha adjacent endothelial cells narrow canals are to be seen, running up to the border of epithelium. These serve for dilating the lumen. This phenomenon is almost exactly as described previously by us for the blood vessels of the human glomus caroticum (ÁBRAHÁM, 1970).

The long pericytes, curved, in accordance with their position, in sickle-form, are similarly full of pinocytotic vesicles. In addition to those described above, there is another feature, namely that the depressions between the protrusions of the endothelial cells are filled in by the protrusions coming from the body of the pericytes. This arrangement may similarly be connected with dilating the lumen and thus with the activity of blood vessels. The nucleus of the pericytes is extremely long, narrow and curved, its chromatin occurring overwhelmingly along the nuclear membrane (Fig. 4).

Nervous system

On the border of the loose and dense coria, resp. within the compact corium, a particularly large mass of neural elements can be found. Apart form the rich receptor system of the external genitals of Mammals, a region like this is hardly known where such an immense mass of neural elements can be seen. Immediately below the epidermis, arranged almost in a single line the Grandry corpuscles, and between, and below these, the Herbst corpuscles, are to be found in a large mass. This may of course, not be a definite regularity, but it should be emphasized that, in the cross-section, two to three Herbst corpuscles fall between any two Grandry corpuscles. To every Grandry corpuscle and every Herbst corpuscle a separate, easily seen nerve fibre is leading. This is, if impregnated successfully, sharply conspicuous. The course of these fibres can easily be followed on one or an other, nerve trunk which wary in thickness. It is, therefore, true to say that here is a real and very sensitive complex of sense organs which is characteristic of the ceroma (ÁBRAHÁM, 1976, Fig. 6).

What, from among the components of this complex, is the function of the Grandry corpuscles, and of the Herbst corpuscles, cannot be deduced without appropriate experiments. It can be supposed however even on the basis of morphological knowledge that the function of the Herbst corpuscles may be more general, these being characteristic generally of birds. They are limited to the ceroma, the mucosa of the oral cavity and the tongue and may serve the functions belonging to these areas. They are supposedly organs of the pressure sense. The Grandry corpuscles may serve a function belonging exclusively to the ceroma of ducks as bodies like these occur

Fig. 4. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Postcapillary vein. L = lumen, E = endothelial cell, P = perycite, N = nucleus, Ic = intercellular diverticulum, V = pinocytotic vesicle, G = Golgi complex, Cm = cell membrane, M = mitochondrium. x32,000

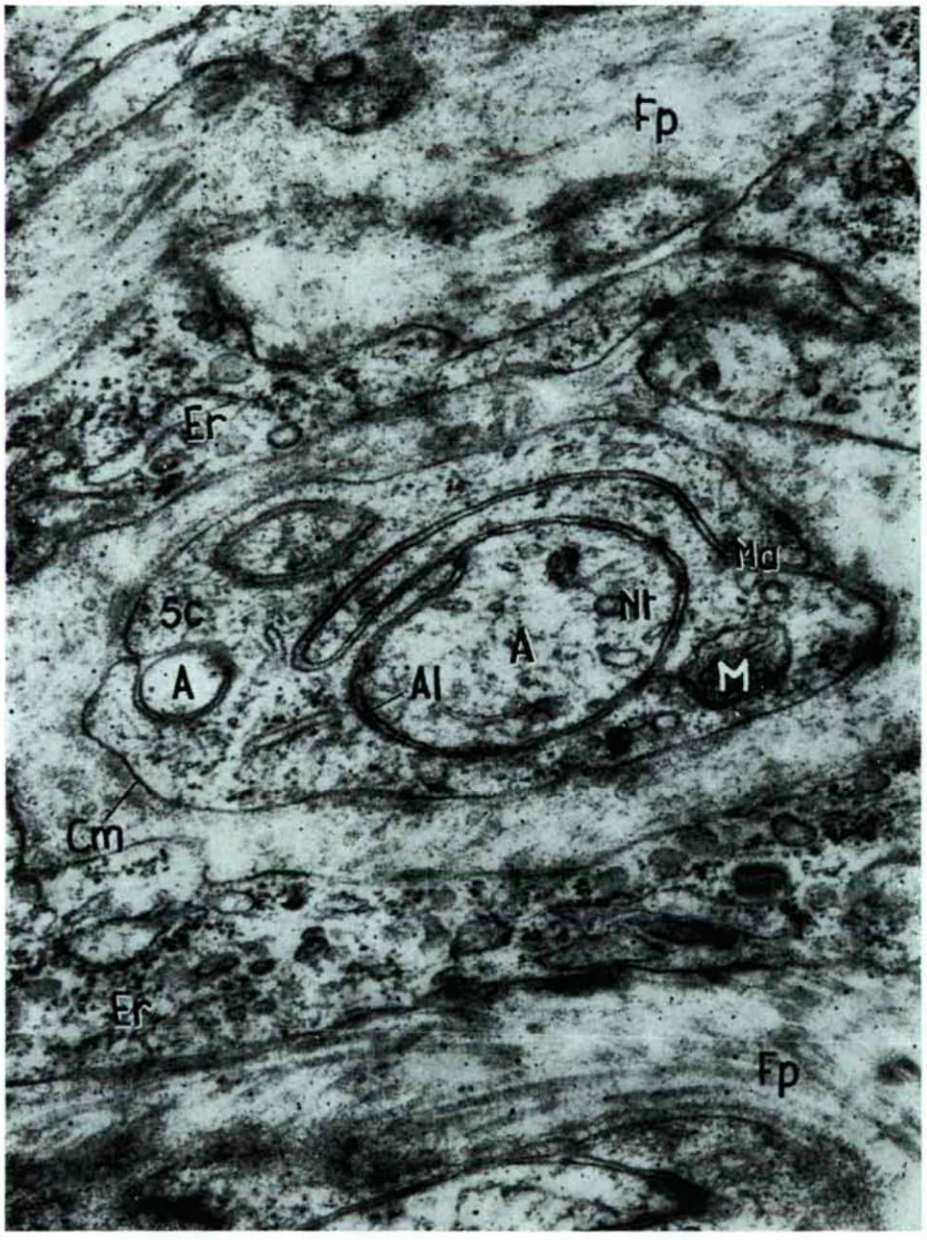

Fig. 5. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Sc = Schwann's cell, Cm = cytolemma, Ma = mesaxon, A = axon, Al = axolemma, M = mitochondrium, Er = endoplasmatic reticulum, Nt = neurotubules, Fp = fibrous tissue cell-process. x120,000

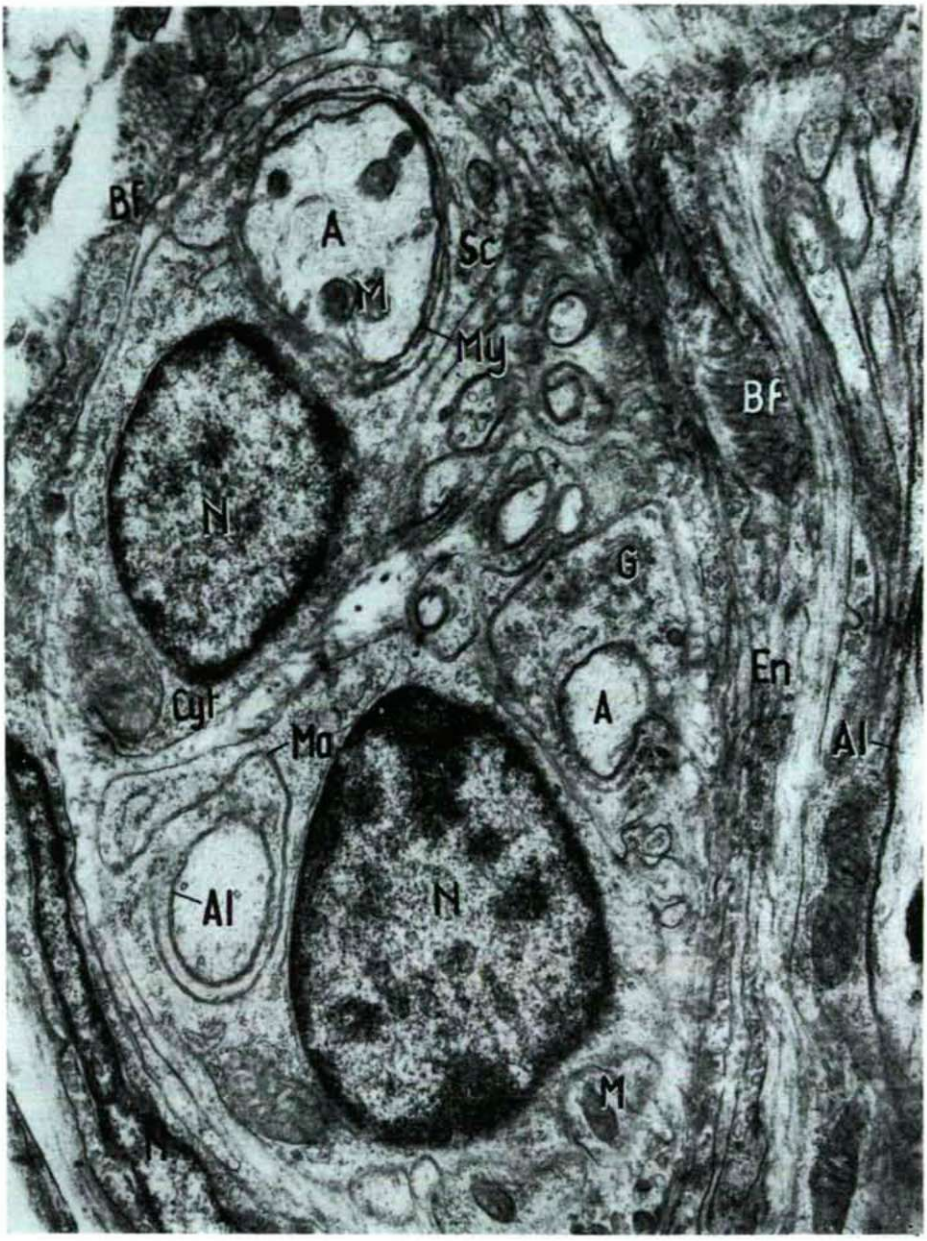

Fig. 6. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Sc = Schwann's cell, Cyt = cytoplasm, G = Golgi complex, N = nucleus, A = axon, Al = axolemma, En = endoneurium, Ma = mesaxon, My = myelin sheath primordium, M = mitochondrium.
x32,000

neither in other organs of ducks, nor in other birds. Or, if they yet occur, they do so only occasionally and in an extremely low number. They are probably organs of touch.

Taking into consideration that in the ceroma both endorgans are together, the question is raised as to what their combined function together and in such a large mass is. As the results of our investigations into Grandry's corpuscles have already been published (ÁBRAHÁM, 1976), we will deal below, apart from the general neural picture, with the structure of the Herbst corpuscles.

General neural picture

As to the general neural picture, the following can be said of it. There are particularly many Schwann's cells, most part of which are full of most forms of mesaxons. Among these are some penetrating only slightly into the cytoplasm, but others which protrude deeply into is (Fig. 5).

There are not infrequently canal systems, forming particular plexuses, ramifying in an extremely rich and complicated way. In the end-part of any canal, in a hemispherical sector, the cross-section of an axon in each of these can be seen well, and in this also the axolemma, within that the filaments, tubuli and in some cases mitochondria. Pictures like this occur in various sizes and forms. It is clearly shown by these systems how the axons are embedded more and more in the cytoplasm of Schwann's cells (ÁBRAHÁM, 1976, Fig. 7).

There are also some pictures, although rather few in which nearly all the phases of the formation of mesaxon are represented. In addition, it can also be seen, how the winding of the mesaxon round the axon-body, and with that the formation of the myelin sheath, begins. This process of winding is to be seen in the left upper corner of the next picture, above the nucleus (Fig. 6).

Further stages in the formation of the myelin sheath are clearly demonstrated in the next Figure in which the course of development of both membranes covering the nerve fibres can be followed exactly. The myelin sheath, already formed in Schwann's cell, the cytoplasm of the cell, its nucleus and nucleolus can be seen. There are also visible the forms of development following this, when the nucleus disappears and the cytoplasm shrinks. At last, the axon, and around it the myelin sheath and the neurilemma, which is a remnant of Schwann's cell-body, are to be seen. The axoplasm is clear and palely filamentous in any nerve fibre. The mitochondria in the axon are polyhedric, their number and situation is rather varied (Fig. 7).

It is clearly shown by the above pictures how the mesaxons are transformed as a result of the axial rotation into a myelin sheath and how Schwann's membrane developes from the remainder of Schwann's cell round the myelin sheath. It is interesting that while in Schwann's cell itself there are but comparatively few mitochondria, there occur — even if rarely — some Schwann membranes, that contain many mitochondria. These assemble in dense groups where they almost touch one another in certain parts of the membrane. On the other hand, in the other larger part of the membrane there can be seen no mitochondria at all (Fig. 8).

In Schwann's cells, apart from the axons, Golgi complexes can be seen in mass. In addition, there are a great many vesicles of changing size. Moreover, there are also ellipsoid bodies of thin wall, containing small corpuscles. The cisternae of the endoplasmic reticula are also visible, and beside these the ribosomes, arranged in a row.

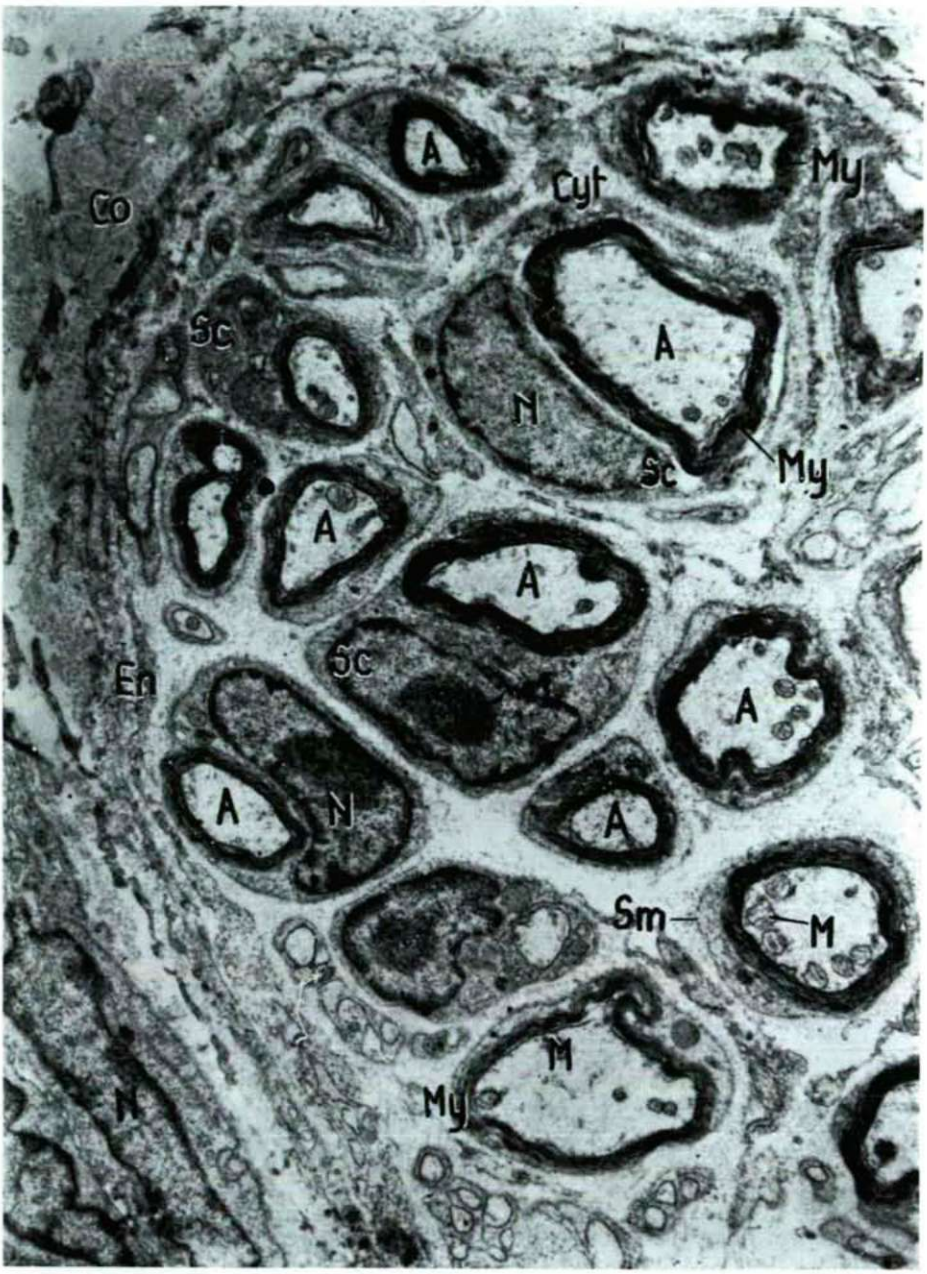

Fig. 7. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii*. Sc = Schwann's cell, Cyt = cytoplsm, N = nucleus, A = axon, My = myelin sheath, Sm = Schwann's membrane, M = mitochondrium, En = endoneurium, Co = collagenous fibre. x = 10,500

The Herbst corpuscle

The Herbst corpuscle was discovered by WILL in 1850. To study the structure of skin, he investigated the skin of the whole body of birds belonging to thirty different species. His aim was to see, how many Herbst corpuscles place on the single marked skin surfaces. He was also interested in the structure, and the differences between the Herbst corpuscle and the Vater—Pacini corpuscle occurring in the higher Vertebrates. To the latter question KÖLLIKER (1854) tried to give an answer.

The Herbst corpuscles were discussed, among others, by LEYDIG (1854, 1868), KRAUSE (1860, 1861), ENGELMANN (1863), HOYER (1864), RAUBER (1867), GOUJON (1869), GRANDRY (1869), IHLDER (1870), MERKEL (1875, 1880), KEY and RETZIUS (1876), HESSE (1878), KRAUSE (1881), LUDWIG FERDINAND von BAYERN (1884), SCHWALBE (1887), DOGIEL (1899, 1904). These authors generally say little about the structure of the endbody, having no procedures or means for approaching the fine structure.

Light-microscopic structure

The thorough description of the end-body is connected with the name of SZYMONOWICZ (1897) who established, on the basis of this studies, performed on the ceroma of the domestic duck, with methyleneblue, that the Herbst corpuscles are ovoid formations and are similar to the Vater-Pacinian corpuscles. MUNGER (1971) names the Herbst corpuscles the "cousins" of the Vater-Pacinian corpuscles. Their longitudinal diameter in the ceroma of the domestic duck varies between 120—160 μ. Their cross-diameter is 70 to 75 μ. The longitudianal diameter is parallel to the surface of skin. The endbody itself consists of two parts that is the central and the periferal part. The central part comprizes the axon, the plasmatic sheath, and the part formed by the tactile cells. The peripheral part consists of laminae, arranged concentrically round the central part.

The axon which is most essential component of the Herbst corpuscle, crosses the external laminar part surrounded by Schwann's membrane and the myelin sheath, and loses its myelin sheath in the internal region, Schwann's membrane reaches as far as the cells covering the plasmatic sheath.

The axon, entering the plasmatic sheath, becomes somewhat thicker and then, preserving this thickness, it runs along the longitudinal axis of the body. At the end, it thickens to a bulb form.

The axon, beginning from the place, where it loses the sheats, is surrounded by a homogeneous plasmatic sheath. Within this, it exists like a finger in a glove (SZIMONOWICZ, 1897).

Along the plasmatic sheath, at each of the borders facing each other on the right and left, there is a cell-row with 6 to 8 cells. The cells are flat and surround the axon in a continuous layer. The nuclei are large and ovoid.

The peripheral part consists of several concentric connective tissue laminae, among which there are few connective tissue cells. The endbody is bordered from outside by a connective tissue layer belonging to the corium, and surrounding the body like an envelope.

The laminae forming the peripheral part of the endbody are considered by

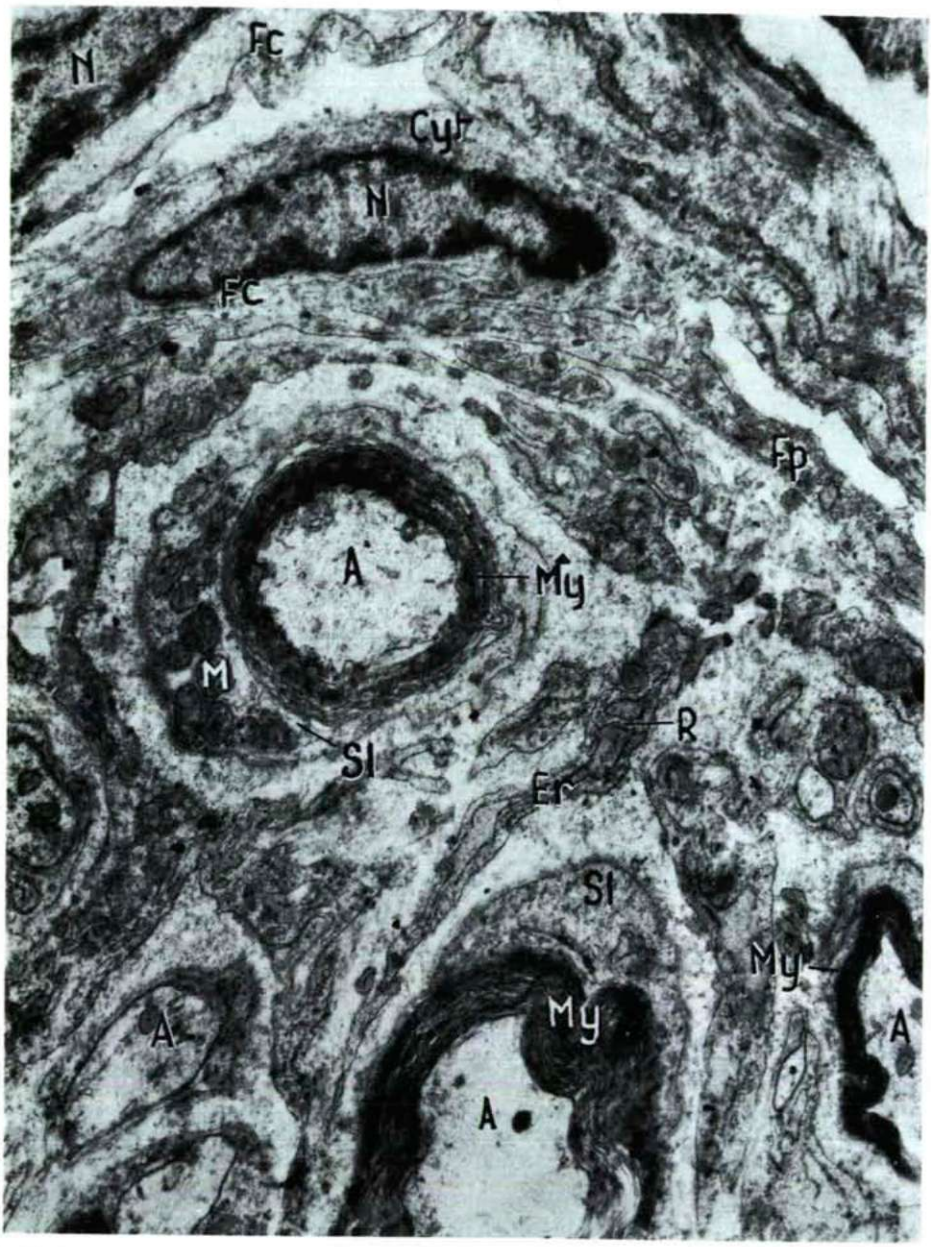

Fig. 8. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* Cyt = cytolemma, N = nucleus, Er = endoplasmic reticulum, R = ribosome, Fp = fibrocyte process, A = axon, My = myelin sheath, Sl = Schwann's membrane, M = mitochondrium. x16,500

SCHUMACHER (1911) and CLARA (1922) as double membranes, enclosing fluid-filled cavities. The latter are, according to BOEKE (1934), kept open by an elastic fibre network. Publications by SZYMONOWICZ (1897) and DOGIEL (1899, 1904) concerning the structure of the Herbst corpuscles are, at any rate, generally confirmed by RUFFINI (1902) HERINGA (1917, 1920), CLARA (1925), and others.

MALINOWSKY (1967) investigated the ceroma of eight bird species, in addition to the skin of the mandible, the eyelid, the crest, the throat, the flap of outer ear, the feathered scalp, the skin of the cloaca-region, the mucosa of the oral cavity, the palate and tongue, in preparations impregnated according to BIELSCHOWSKY—GROS. He distinguished between three types of Herbst corpuscles found at the places investigated. For the classification he chose as parameters the relation between lengthy and breadth, number and form of nuclei, and the arrangement of the central part named inner bulb.

SAXOD (1973) distinguished three parts in the Herbst corpuscle on the basis of light microscopic investigations into the Peking duck, the white Leghorn chicken and the Japanese quail. One of these is the central part consisting of two cell-rows, and is called the inner bulb. The nuclei of cells occur on both sides, along the sensory nerve fibre running towards the axon. The second part is the inner cavity filled in by a system consisting of flat laminae supported by collagenous fibres. The third component is the external laminar sheath.

We could not identify these parts in our preparations stained with haematein and eosin. In our pictures not more than one part with nucleus and one with lamina could be distinguished, and even in these, the structure could not be recognized.

For clarifying the structure, a greater possibility was afforded by the silvered preparations made according to the procedure of BIELSCHOWSKY and ÁBRAHÁM. In these, the three parts named by SAXOD, namely the inner bulb, the inner cavity and the outer sheath can be recognized and delimited well towards one another although in respect to the details these remained in doubt in more than one respect.

In our silvered preparations, in the inner bulb the inner bulb cells, the inner bulb laminae, and the axon can be seen. But only the nuclei of the inner bulb cells are clearly visible. The cytoplasm presents itself in the form of pale and weak threads. One thing is extremely clear in this respect namely that the cells are in close connection, apparently in continuity with one another.

The laminar system of the inner bulb is striking but it cannot be established from this picture that the parallel laminae of the system originate from the inner bulb cells.

The axon, forming varices in the inner cavity begins from the inner bulb cells, becomes an increasingly thick homogeneous structure eventually assuming a bulb-like shape. In the sector of the axon falling in the region of the inner cavity, between two varices, on each sides, a large elliptical nucleus takes place. These are considered as the nuclei of wandering cells which have migrated here from among the inner bulb cells.

The inner cavity in the picture seems to be for most part homogeneous. There are to be seen occasional nucleus-like formations but it cannot be established whether these are nuclei or fragments of a lamina. It is, however, obvious that these fragments are in a concentric position and therefore can be qualified as laminae.

In the external laminar sheath the collageneous fibres are arranged in two or

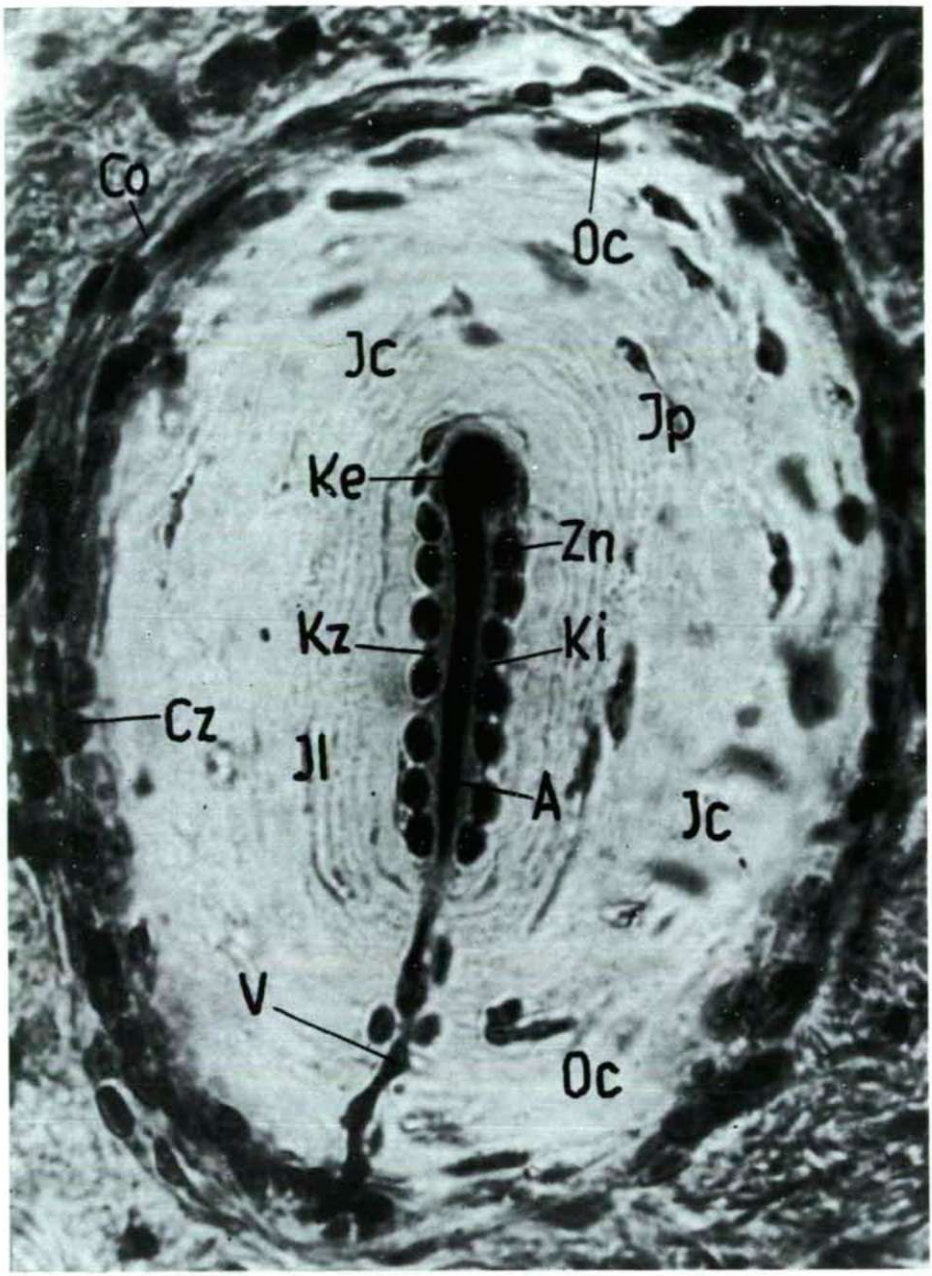

Fig. 9. Mallard *(Anas platyrhyncha)* Ceroma. The Herbst corpuscle. Ki = internal knob, Kz = internal knob cell, Zn = internal knob nucleus, A = axon, Il = internal knob lamina, Ic = internal cavity, Ip = internal-cavity plate, Oc = outer capsule, Co = connective-tissue fibre, Cz = connective-tissue cell, V = varix. Bielschowsky-Ábrahám's procedure. x1200

three rows and along these the connective tissue nuclei can easily be observed. Among them there are large elliptical forms which are almost identical with the nuclei of the inner bulb cells, and also elongated sharpened forms (Fig. 9).

Ultrastructure

In spite of the fact that many researchers have tried to recognize the structure of the laminar nerve endbodies, and among these that of the Herbst corpuscles, the endbodies have remained, in their entirely, unknown. The real structure was only discovered with the help of the electron microscope. This was a new world for everybody who was interested in the relations of end-connections in the nervous system and in the particular arrangements enabling the reception of stimuli in the sensory nerve fibres. It is natural that these investigations have started comparatively late since those enjoying the possibility of performing electron-microscopical investigations, were first of all interested in examining the central nervous system, and the higher brain activity. The electron-microscopic examination of the lamellated end-bodies and among these of the Herbst corpuscles, is essentially connected with the names of SAXOD (1969, 1970, 1973), GOGLIA (1969), NAFSTAD and ANDERSEN (1970), HALATA (1970), and GREGORY (1973). The results of investigations by these authors, are interesting and valuable but — as we read also in Saxod's comprehensive work (1973) — there remained still much to do, mainly in the domain of the neuron connection.

Cells of the inner bulb

The inner bulb consists of two cell rows. These cells are generally named sensory or signalizing cells (indicators). The nuclei of cells occur along the sensory nerve terminals, on both sides symmetrically. The number of cells was generally twenty in the species investigated. The cells are long bodies with processes, tapering at both ends. The nucleus is largely hemi-spherical, casually polyhedric and irregular, its margin towards the nerve fibre being hollowed out form a crescent-shape. The external surface of any cell touches some cell of the inner cavity. From its internal surface, 20 to 50 laminae originate. These taper ramifying or returning to the place of their origin. The laminar system of each cell is connected with the laminar system of any cell taking place before and behind it in line, as well as with the laminae of the cell row on the other side (Fig. 10). Thus in the photographs the picture of a laminar system suggests that is concentric in the cross-section of the body and parallel in its longitudial section. In the laminae, ribosomes and multivesicular bodies are frequent. Among the laminae, large ovoid vesicular groups appear here and there in pairs.

The nerve terminal

The Herbst corpuscle is innervated by a single myelinated fibre of trigeminal origin, forming several gyruses before entering the external sheath. It loses its myelin sheath and Schwann's membrane before entering the inner bulb. Throughout its further course it is a bare axon. SAXOD (1973) saw in it short spines and meandering processes but we have not observed any of these. The nerve fibre doubles in thick-

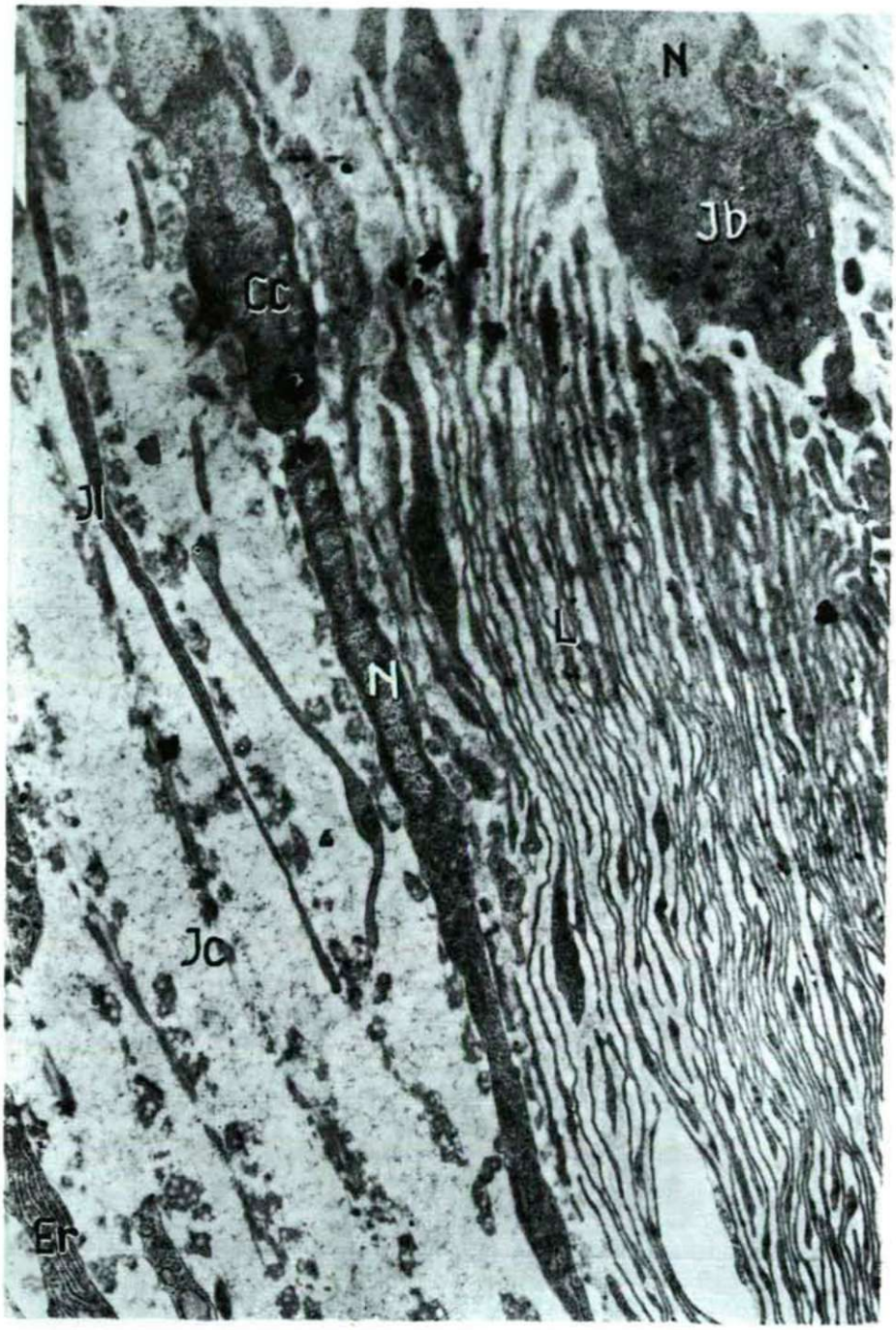

Fig. 10. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii*. The Herbst corpuscle. Ib = internal butt cell, N = nucleus, L = internal butt lamina, Ic = internal cavity, Cc = central cavity cell, Il = internal cavity lamina, Er = endoplasmatic reticulum. x16,500

ness at about the end of the body, and becomes ovoid, forming a neural terminal disk which grows first narrower and then broader.

The nerve fibre and, of course, the nerve terminal, too, are limited by the sharp homogeneous axolemma of equal thickness towards the cytolemma of the processes of the sensory cells. In the nerve fibre, and also in the nerve terminal, there are but few elongated mitochondria with crests, limited by a double membrane. The crests run lengthwise and each has a double wall. The walls are separated from one another by an obvious gap (Fig. 11).

In the axoplasm, in the terminal area, and in the nerve fibre itself, there are several roundish vesicles. Among these there are small forms with obvious lumens, larger empty forms, and also forms of dense core type, forming major groups. The last show a great similarity to the neurosecretory granules. In addition, we should point out the microvesicular bodies which are filled with vesicles of very different sizes. These include the elliptical organella enclosed with crinkled sheaths, containing roundish vesicles of different diameters. In the axoplasm, mainly in the vicinity of the end-disc, there are a great many neurotubuli, runing parallel with one another.

The axolemma is sharply delimited towards the cytolemma covering the laminae. The gap lying between them is obvious is of the same breadth in its entire course and thoroughly empty. There is no contact between the two membranes. No thickening can be seen on any of the membranes. The nerve ending itself is a splendid example of what the afferent synapsis consists of, and how the nerve fibre joins with the sensory cells supplying it with impulse conduction (Fig. 12). SAXOD (1973) found junctions of zolula occludens and zonula adherens type between the membranes covering the laminae and the axolemma. We have not found anything like this nor any of the nerve-like fibres, observed by NAFSTAD, ANDERSEN (1973) in the laminar system of sensory cells.

Taking into consideration that any sensory cell of the inner bulb has twenty of more processes, that several of these ramify, and that the laminar system of any cell is joined with the laminar system of the cells before and behind it, as well as to the laminar system on the other side of the nerve terminal, we have an idea of what an almost inexplicably complicated function system may exist even in a single sensory cell and how terribly sophisticated the mechanism starting the working process of the impulse conduction, ensuring its continuity, and furthering the stimulus to the nerve centres may be.

The internal cavity

The internal cavity consists of several laminae of varying breadth, separated from one another by a cavity system filled with fluid. The laminae are the cells of the internal cavities, standing with their processes in loose connection with one another. They are similar to the fibroblasts. Their processes enter the internal cavity, going round the inner bulb. There can be distinguished three groups of the lamina-shaped processes:

Those belonging to the first group are bodies of peculiar form and structure. They contain many voluminous endoplasmic reticula, delimited partly or wholly by a ring of ribosomes, as well as mitochondria of particular type, Golgi complexes, and here and there some vesicles. The characteristic ramifications and lateral out-

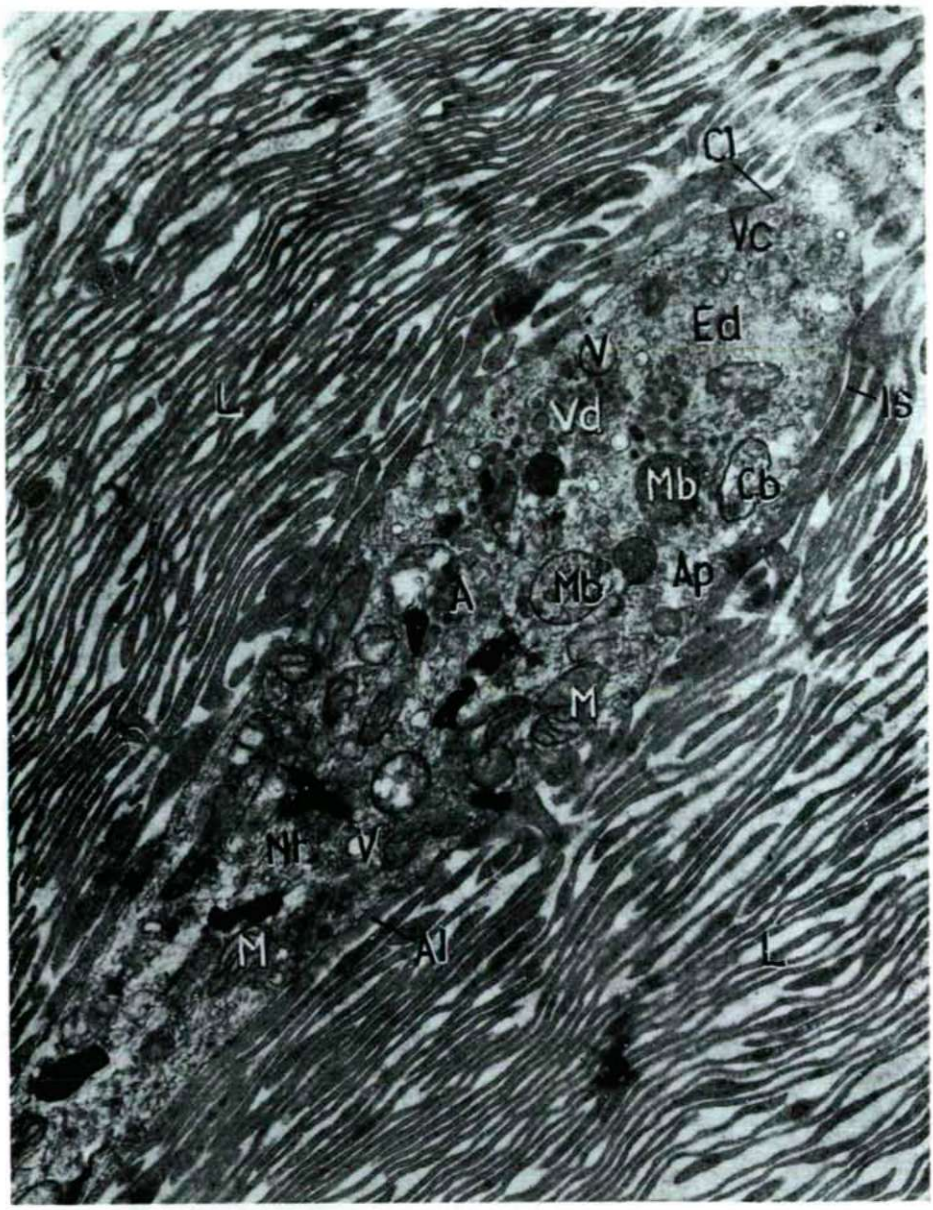

Fig. 11. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* The Herbst corpuscle. L = internal butt lamina, Mb = multivesicular body, Cl = cytolemma, Al = axolemma, Is = intersynaptic space, Ed = end disc, A = axon, Ap = axoplasm, M = mitochondrium, Nt = neurotubulus, Vd = dense core vesiculum, Cb = cylindrical body, Vc = clear vesicle, V = vesicle. x24,600

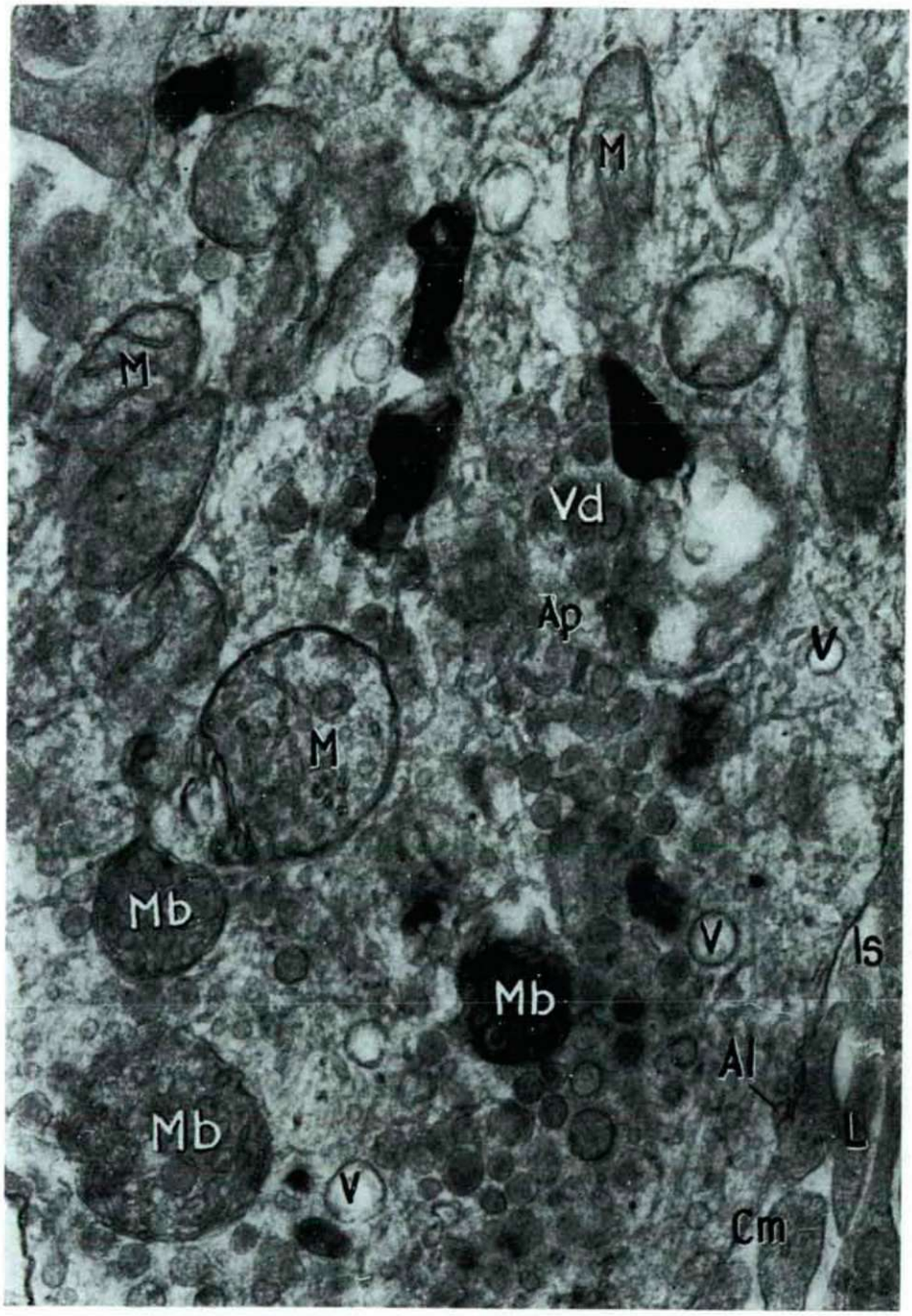

Fig. 12. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* The Herbst corpuscle. L = internal-butt lamina, Cm = cytolemma, Is = intersynaptic space. Al. = axolemma, Ap = axoplasm, Vd = dense core vesicle, Mb = multivesicular body, V = vesicle, M = mitochondrium. x85,000

Fig. 13. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii.* The Herbst corpuscle. L = internal-butt lamina, Lc = internal cavity lamina, M = mitochondrium, G = Golgi complex, V = vesicle, R = ribosome. x32,000

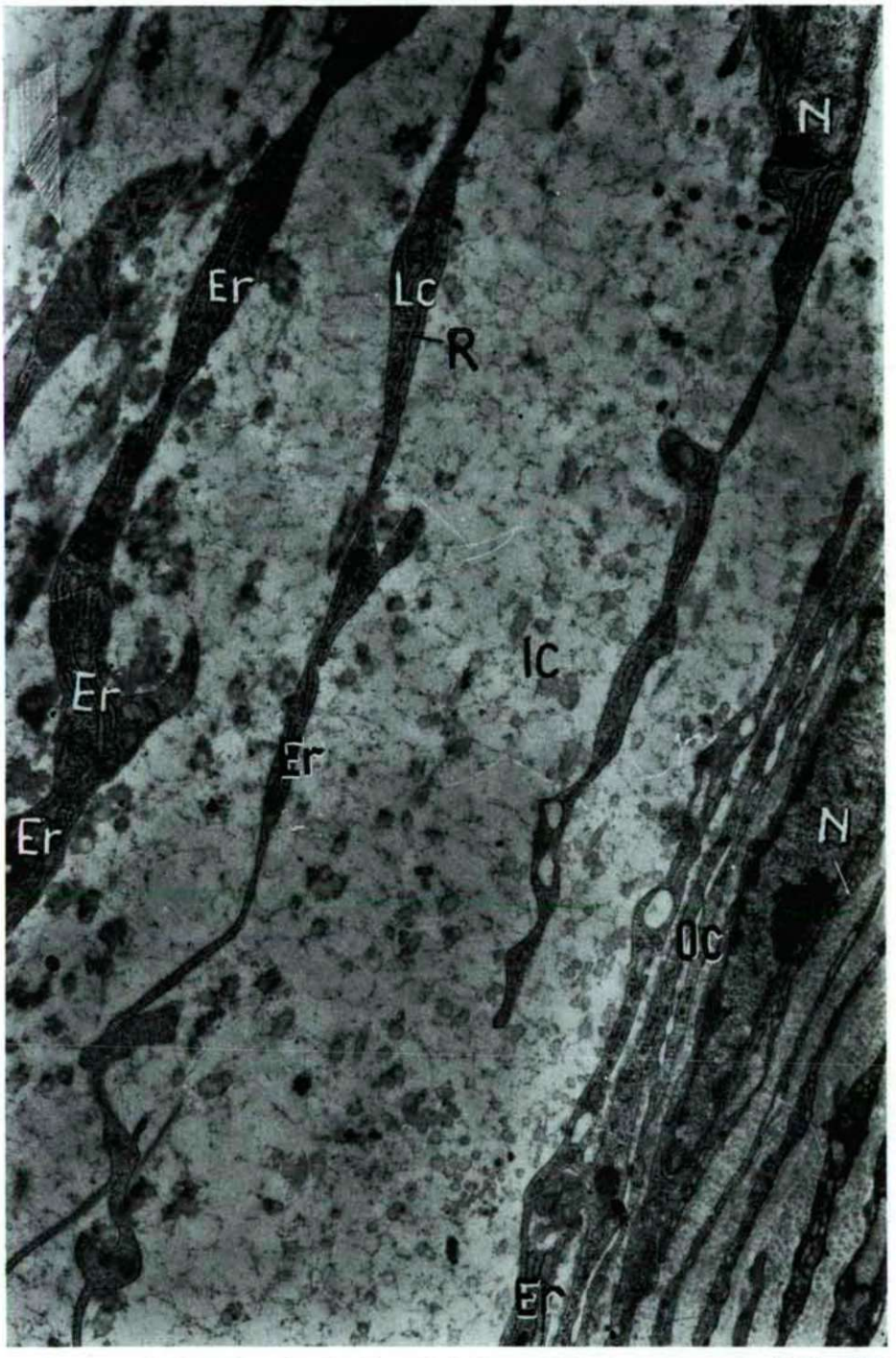

Fig. 14. Domestic duck *(Anas boschas domestica)* Ceroma. *Stratum compactum corii*. The Herbst corpuscle. Ic = internal cavity, Lc = lamina of the cavity, Oc = outer capsule, Er = endoplasmic reticulum, R = ribosome, N = nucleus. x16,500

growths are frequent. In the empty space, multivesicular corpuscles are not infrequent (Fig. 13).

The laminae to be classified into the second group are bodies of straight course, ending in points. They are characterized by cisternae finding the way back and by ribosomes following the cisternae in a row.

The form of laminae to be classified into the third group is characterized by a nucleus rounded at one end and elongated at the other, with comparatively little chromatin. The cytoplasm is a very small, narrow strip on the nucleus, in other places it forms some knobs, repeated almost regularly. In the thin, initial sector of the lamina, the parallel running cisternae of the endoplasmic reticulum manifest themselves in the cytoplasm and the ribosomes form dense rows. A great number of rows of ribosomes are also to be found, which are not connected with the cisternae.

The external sheath

The external sheath of the domestic duck consists of 10 to 13 concentric laminae, separated from one another by collagenous fibrous bundles. The bundles run concentrically. Their thickness varies due to the volume of the cavities between the laminae. The number of the collagenous fibres greatly increases towards the stratum laxum corii. The laminae are comparatively narrow, but larger forms also appear, mainly in the middle part of the sheath. Their cytoplasm is sponge-like, containing several empty vesicles of different forms and sizes. Some of the laminae ramify. There are also a very few which have two nuclei. The nuclei are long, one end being obtuse, and the other sharpened. The nuclear membrane is well-defined. Part of chromatin is joined with the nuclear membrane while the remainder appears in the form of tiny granules (Fig. 14).

The laminar system, occuring in the stratum compactum, is delimited by the loose fibrous system of the stratum laxum corii and by a large mass of the characteristic fibroblasts.

Discussion

There is hardly any detail of the nervous system in which the research workers of different ages would have been so interested as the sensory fibres and the sensory terminal apparatuses which in the organs of surface position, primarily in the common integument, single or covered with different membranes, serve for receiving and conducting impulses originating from the environment. We should have to gave quite a long list of prominent and devoted researchers even if we wanted to enumerate only the names of those trying to recognize the structure of receptor apparatuses falling to the region of the common integument, and trying on this basis to draw conclusions concerning their activity.

The series of problems — the components of which were discovered and discussed with the help of the methods and means available at the different times — was always to recognize the following: Where are the sites where the sensory nerve fibres and receptors are situated, what are the tissue groupings which surround the nerve fibres and nerve terminals respectively, connecting these with the environment, and lastly, are there in the nerve fibre any organelles by means of which they respond to the effects of the environment with a particular sensitivity?

Most of the problems had already been solved by the middle of the Nineteenth

Century using light- microscopy, but there remained many questions which could only be solved with the electron microscope. This latter has opened in many areas and several respects quite a new world for the researchers interested. The electron microscope has revealed the laminar systems surrounding the nerve fibres, and the nerve fibre itself. Some problems have remained, all the same, requiring other devices and conceptions before they can be solved.

The problems of the laminae of Herbst's, Vater-Pacini's and Grandry's endbodies — which under a light-microscope did not appear clear at all — now seem to be solved. The structure of the sensory cells formed into a line in the central part of the Herbst corpuscles came to light, and from this the form of connection of the laminar system of the inner bulb with the nerve fibre also became clear. The laminar system of the inner cavity and external sheath was, correctly interpreted.

The electron-microscope pictures, illustrating the structure of the Vater-Pacinian laminar system, justified the separation of the external and internal sheaths. At the same time they showed how much the cells forming the laminar system of the Pacinian corpuscles differ from the sensory cells and laminar system of the Herbst corpuscle (CHOUCHKOV, 1971). Although in the structure of the sheath, and in the connection of the sensory cells and satellite cells there is some similarity, the covering, enclosing the sensory fibre in the Grandry corpuscle shows quite another picture.

The electron microscope has presented a different picture to the world, concerning the position of the nerve fibre runing along the endbodies. The bare axon of the Herbst corpuscle, preserving its original thickness, runs through the middle of the inner bulb up to the third-fourth part of the endbody. Here, close to the end, it widens, then narrows and, finally, ends rounded as a bulb. DOGIEL (1899) and SAXOD (1973) found tiny protrusions and processes on it. We have not observed anything like these and found the axolemma smooth, homogeneous and of equal thickness throughout its whole length. The gap between the axolemma and cytolemma is spacious and constant. SAXOD (1973) found some homogeneous granular substance in it but we have not seen anything of this type.

The axon of Pacinian endbody contains dispersed mitochondria, neurofilaments, and neurotubuli. Its ending is sometimes double, occuring at the pole of the endbody, between the internal and external sheath (CHOUCHKOV, 1971). In some regions of the axolemma some desmosome-like formations were observed, but synaptic formations were not found. In the bare axons running through the Grandry corpuscles with a single sensory cell, the mitochondria form a chain. On the other hand, in the endbody with two sensory cells, starting from the site of ramification mitochondria are entirely missing (ÁBRAHÁM, 1976).

In the nerve terminals of the Herbst corpuscle there are many mitochondria, situated round the neurotubuli. There are several vesicles of synaptic-vesicle type. The number of dense core vesicles is much smaller (SAXOD, 1973). According to our investigations, there are few mitochondria but many roundish vesicles. Among these there are some smaller ones, with an empty lumen delimited by a sharp membrane, and also larger forms of dense core type. The latter form groups and show a great similarity to the neurosecretory granules. There are some round bodies delimited by a sharp wall, full of vesicles of different sizes. There are also some particular elliptical bodies enclosed by a sheath, containing some vesicles of different diameters, and there are several neurotubuli parallel in position.

CHOUCHKOV (1971) found some axoplasmatic protrusions in the broadened endbulb of the central nerve fibre of the Pacinian corpuscles. These consist of neurofilaments with varying position and form. Some of them are elongated others are cone-shaped, and the remainder are rounded. They are situated between the collagenous fibrils at an equal distance from one another, being connected together chainlike. In the protrusions there are no mitochondria, endoplasmic reticulum, or lysosomes. But at the point where the protrusions begin, the mitochondria form a dense mass.

In the axoplasm of the terminal ramuli of the Grandry corpuscles with double sensory cells, there are also neurofilaments, synaptic vesicles, and granular vesicles (ÁBRAHÁM, 1976). SAXOD (1973) observed various juction-forms between the sensory cell and the nerve terminal. We have not seen any junctions. According to our investigations, the space between the membranes is completely empty. We consider the connection as a typical parallel contact.

In the axoplasm of the Grandry corpuscles with one sensory cell, and in the area of the sensory disc, there are so many mitochondria that they are almost in contact with one another. Immediately under the axolemma, vesicles of synaptic type and microvesicular corpuscles are also to be seen. The axolemma is sharp and homogeneous, and both of its margins are smooth. The cytolemma is well-delimited, and the gap between the membranes is obvious, spacious, empty, and of equal diameter through its entire course. The connection between the two membranes is qualified as a parallel contact. We have seen a thickening only once in the axolemma and opposite to it, in the cytolemma, near to its end. It is difficult to decide whether this is — is spite of the fact that below the thickening in the axolemma synaptic vesicles exist — a synapsis or a desmosome *(zonula adherens)*, but as there is no grouping of synaptic vesicles on either side, we consider the form of junction as a desmosome.

ANDERSEN and NAFSTAD (1968), and NAFSTAD and ANDERSEN (1970) saw two nerve fibres in the Herbst corpuscle. One of these was the central afferent fibre, while the other was found in the laminar system of the inner bulb and qualified as an efferent fibre. In the Pacinian corpuscle, the same situation was found by CHOUCHKOV (1971) who similarly speaks of afferent and efferent fibres. He found the efferent fibres between the external and internal sheaths.

The problem is not new. It has already been observed by more than one worker that the receptors contain both afferent and efferent synapses. From among those doing pioneering work in this area, the names of SMITH (1956), WERSÄLL (1956, 1961), BAIRATI (1961), ENGSTRÖM (1961), JURATO (1962), FLOCK, KIMURA LUNDQUIST and WERSÄLL (1962), and SMITH and RASMUSSEN (1965), are to be mentioned. It became known following their activity that in the vestibular epithelium of the higher Vertebrates, sensory cells of two different types can be found. These were designated as hair cells of first and second type. This was followed by the discovery that the hair cells of first type were entirely surrounded by the centripetal nerve fibre the scarcely granulated calix and the hair cells of second type were supplied with two different nerve terminals of different structure, in sharp contrast to each other. One of these is scarcely granulated, being in synaptic contact with the membrane of the sensory cell. This ending — judged by its structure — is postsynaptic. The other ending which appears in lower number is circular and densely granulated (ENGSTRÖM, ADES, HAWKINS, 1965). It is in contact with the surface of the sensory cell and, in the region of contact, a distinct thickening is visible both in the plasma-

membrane and in the axolemma. This synapsis form is qualified as efferent. The mammalian vestibular epithelium has double innervation verified by JURATO (1962) who observed, after the olivocochlear bundle being transect, some synaptic elements of the cochlear receptors degenerate.

Similar problems were dealt with by HAMA (1969) who — in the course of his investigations into the auditory spot *(macula acustica)* of the goldfish *(Carassius auratus)* — found two forms of connection between receptor cells, and of nerve terminals. In one of these, the electron density of both the nerve terminal and the membrane of the receptor cell is increased. The electron dense material is mainly stored in large amounts in the axolemma. In the sensory cell, the accumulation is slighter. In the receptor cell, near the plasma-membrane, a roundish electron dense body can be observed, bordered by a layer consisting of vesicles.

In the second form of connection, there aren't any specializations, either in the plasma-membrane of the receptor cell, or in the axolemma, which are generally characteristic of synapses. Here the two synaptic membranes shut each other, and the nerve terminal is full of synaptic vesicles, some of which are open towards the intersynaptic space. Among the synaptic vesicles there are also a few dense core vesicles.

Concerning the activity of the two synapsis-forms, HAMA, has the following — in our opinion right — ideas. The first synapsis-form, where the groups of synaptic vesicles are in the receptor cell and the thickening is more obvious on the side of the nerve terminal than on the side of the receptor cell, it is an afferent synapsis in which the stimulus is transferred from the receptor cell to the nerve terminal. In the second synapsis-form, the vesicle groups take place in the nerve terminal. Consequently, the direction of impulse transfer is from the nerve terminal to the plasm of the sensory cell. The contact qualifies, therefore, as an efferent synapsis. In respect of functioning it is named inhibitor.

ÁBRAHÁM (1968, 1969, 1970a, b) described from the human glomus caroticum some synapses, clearly showing every feature of the efferent synapses. Taking into consideration that the glomus caroticum is a chemoreceptor, as verified structurally and functionally, the question is raised, as to what is the function of the efferent synapsis. It is however generally, and unanswered question what role the efferent synapses in the receptors play. They may be inhibitors or moderators but they may in addition, serve another function. At any rate, as we cannot give a generally acceptable reply to this question, we are also at fault for drawing an uniform picture of the structure of the peripheral sensory nerve terminals, of junctions, and of the general structure of the afferent synapses.

References

ANDERSEN, A. E., NAFSTAD, P. H. I. (1968): An electron-microscopic investigation of the sensory organs in the hard palate region of the hen *(Gallus domesticus)*. — Z. Zellforsch. *91*, 391—401.

ÁBRAHÁM, A. (1968): Electron-microscopic investigations on the human carotid body (Preliminary communication). — Zschr. mikr.-anat. Forsch. *79*, 309—315.

ÁBRAHÁM, A. (1970)a: Elektronmikroskopische Untersuchungen an menschlichen Karotiskörpern. — Zschr. mikr.-anat. Forsch. *81*, 413—453.

ÁBRAHÁM, A. (1970)b: Recherches ultrastructurales sur les terminaisons nerveuses du "corpuscle carotidien" humain 54. — Association des Anatomistes *146*, 393—400.

ÁBRAHÁM, A. (1976): Elektron mikroszkópos vizsgálatok a házikacsa cerómáján, különös tekintettel a Grandry-féle testekre (Electron-microscopic investigations into the cerome of the domestic duck, with particular regard to the Grandry corpuscles), — Állattani Közl. 63, 15—37.

BAIRATI, A. (1961): Recentes connaissances sur la structure submicroscopic des organes du vestibule. — Acta oto-laryng. Suppl. *163*, 9.

BOEKE, J. (1925—26): Die Beziehungen der Nervenfasern zu den Bindegewebselementen und Tastzellen. — Zschr. mikr.-anat. Forsch. *4*, 448—509.

BOEKE, J. (1934): Freie Nervenendigungen und Endorgane sensibler Nerven. In: Handbuch der vergleichenden Anatomie der Wirbeltiere. — Zweiter Band, 2. Hälfte, 855—878.

BOTEZAT, E. (1911): Knäuleartige Nervenendigungen in der Vogelhaut. — Anat. Anz. *39*, 143—148.

BOTEZAT, E. (1906): Die Nervenendeapparate in den Mundteilen der Vögel und die einheitliche Endigungsweise der peripheren Nerven bei den Wirbeltieren. — Z. wiss. Zool. *84*, 205—360.

BURNS, R. B. & WIGHT, P. A. (1970): The distribution of Herbst corpuscles in the foot of the domfowl *(Gallus domesticus)*. Res. vet. Sci. *11*, 585—587.

CAUNA, N. (1962): Functional significance of the submicroscopial, histochemical and microscopical organizations of the cutaneous receptor organs. — Anat. Anz. *111* Erg, H. 181—197.

CAUNA, N. (1966): Fine structure of the receptor organs and its probable functional significance. — Ciba Symp. "Touch, heat and pain", 117—127. London, Churchill.

CAUNA, N. & ROSS, S. L. (1960): The fine structure of Meißner's touch corpuscles of human fingers. — Cell Biol. *8*, 467—482.

CHOUCHKOV, H. N. (1971): Ultrastructure of Pacinian corpuscle in men and cats. — Zschr. mikr.-anat. Forsch. *83*, 17—32.

CLARA, M. (1925): Über den Bau des Schnabels der Waldschnepfe *(Scopolax rusticola* L.) — Zschr. mikr.-anat. Forsch. *3*, 1—108.

DIJKSTRA, C. (1933): Die De- und Regeneration der sensiblen Endkörperchen des Enteschnabels (Grandry- und Herbst-Körperchen) nach Durchschneidung des Nerven, nach Fortnahme der ganzen Haut und nach Transplantation des Hautstückchens. — Zschr. mikr.-anat. Forsch. *34*, 75—158.

DOGIEL, A. S. (1899): Zur Frage über den Bau der Herbstschen Körperschen und die Methylenblaufixierung nach Bethe. — Z. wiss. Zool. *66*, 358—376.

DOGIEL, A. S. & WILLANEN, K. (1900): Die Beziehungen der Nerven zu den Grandryschen Körperchen. — Z. Wiss. Zool. *67*, 349—360.

DOGIEL, A. S. (1904): Über die Nervenendigungen in den Grandryschen und Herbstschen Körperchen im Zusammenhange mit der Frage der Neuronentheorie. — Anat. Anz. *25*, 558—574.

DOSTOJEWSKIJ, A. (1886): Über den Bau der Grandryschen Körperschen. — Arch. mikr. Anat. *26*, 581—591.

ENGSTRÖM, H. & WERSÄLL, J. (1958): The ultrastructural organisation of the organ Corti and of the vestibular sensory epithelia. — Exp. Cell. Res. Suppl. *5*, 460.

ENGSTRÖM, H. (1961): The innervation of the vestibular sensory cells. — Acta oto-laryng. Suppl. *163*, 30.

ENGSTRÖM, H., ADES, H. W. J. E. & HAWKINS, J. R. (1965): The vestibular sensory cells and their innervation. Modern Trends in Neuromorphology. — Symposia Biol. Hung. *5*, 21—41. Budapest.

ENGSTRÖM, H (1958): On the double innervation of the sensory epithelia of the inner ear. — Acta oto-laryng. *49*, 109.

ENGSTRÖM, H. (1961): The innervation of the vestubular sensory cells. — Acta oto-laryng. Suppl. *100*, 30—41.

FITZGERALD, M. J. T. (1962): On the structure and life history of bulbous corpuscles *(Corpuscula nervorum bulboidea)*. — J. Anat. (Lond.) *96*, 189—208.

FLOCK, A., KIMURA, R., LUNDQUIST, P. G. & WERSÄLL, J. (1962): Morphological basis of directional sensitivity of the outer hair cells in the organ Corti. — J. acoust. Soc. Amer. *34*, 1351.

GEBERG, A. (1893): Über die Innervation der Gaumenhaut der Schwimmvögel. — Intern. Nachr. Anat. Physiol. *10*, 205—240.

GOUJON, E. (1869): Sur un appareil de corpuscles tactiles situé dans le bec des perroquets. — J. anat. physiol. *6*, 449—455.

GRANDRY, M. (1896): Recherches sur les corpuscles de Pacini. — J. Anat. Physiol. *6*, 390—395.

GREGORY, J. E. (1973): An electrophysiological investigation of the receptor apparatus of the ducks bill. — J. Physiol. *229*, 151—164.

HAMA, K. (1969): A study on the fine structure of the saccular macula of the gold fisch. — Z. Zellforsch. *94*, 155—174.

HESSE, FR. (1878): Über die Tastkugeln des Entenschnabels. — Arch. Anat. Entw. gesch. 288—318.

HINSKI, O. B. (1966): Some problems of the receptor physiology. — In the nerve cell. Leningrad. USSR. 187—221.
IHLDER (1870): Die Nerven-Endigung in der Vogelzunge. — Arch. Anat. Physiol. 238—250.
JURATO, S. (1962): Efferent fibres to the sensory cells of Cortis organ. — Exp. Cell. Res. *27*, 162—164.
KIMURA, P. & J. WERSÄLL (1962): Termination of the olivo-cochlear bundle in relation to the outer hair cells of the organ of Corti in guinea pig. — Acta oto-laryng. *55*, 11—32.
KÖLLIKER, A. (1854): Einige Bemerkungen über die Pacinischen Körperchen. — Z. wiss. Zool. *5*, 118—122.
KRAUSE, W (1881): Die Nervenendigungen innerhalb der terminalen Körperchen. — Arch. mikr. Anat. *19*, 53—136.
KROGIS, A. (1931): On the topography of Herbst's and Grandry's corpuscles in the adult and embryonic duck-bill. — Acta zool. Stockholm *12*, 241—263.
KULTSCHIZKY, N. K. (1884): Über den Bau Grandryscher Körperchen. — Arch. mikr. Anat. *23*, 358—379.
LEYDIG, FR. (1854): Über die Vater-Pacinischen Körperchen der Taube. — Z. wiss. Zool. *5*, 75—86.
LOEWENSTEIN, O. H. P. OSBORNE & WERSÄLL, J. (1964): Structure and innervation of the sensory epithelia in the labyrinth of thornback ray *(Raya clavata)*. — Proc. roy. Soc. R. *160*, 1—12.
LUDWIG FERDINAND, PRINZ v. BAYERN (1884): Über Endorgane der sensiblen Nerven in der Zunge der Spechte. — Sitzungsber. d. k. bayer. Akad. d. Wissensch. math.-physik. Klasse. München, 183—192.
MALINOWSKY, L. (1967): Die Nervendkörperchen in der Haut von Vögeln und ihre Variabilität. — Zschr. mikr.-anat. Forsch. *77*, 279—303.
MERKEL, FR. (1875): Tastzellen und Tastkörperchen bei den Haustieren und beim Menschen. — Arch. mikr. Anat. *11*, 636—652.
MERKEL, FR. (1878): Die Tastzellen der Ente. — Arch. mikr. Anat. *15*, 415—427.
MUNGER, B. L. (1965): The intra-epidermal innervation of the snout skin of the opossum. A light- and electron-microscopic study with observations on the nature of "Merkel's Tastzellen". — Cell. Biol. *26*, 79—96.
MUNGER, B. L. (1966): The intra-epidermal innervation of the snout skin of the opossum. — Ciba Symp.: "Touch, heat and pain" 129—130. London, Churchill.
NAFSTAD P. H. & ANDERSON A. F. (1970): Ultrastructural investigation of the innervation of the Herbst corpuscle. — Z. Zellforsch. *103*, 109—114.
NOWIK, K. (1910): Zur Frage von dem Bau der Tastzellen in den Grandryschen Körperchen. — Anat. Anz. *36*, 217—225.
PEASE, D. C., QUILLIAM, T. A. (1957): Electron microscopy of the Pacinian corpuscle. — Biophys. biochem. Cytol. *3*, 331—342.
POLACEK, P. (1966): Receptors of the joints. Their structure, variability and classification. — Facult. med. Brunensis, Brno.
QUILLIAM, T. A. & ARMSTRONG, J. (1961): Structural and denervation studies on the Herbst corpuscle. In: "Cytology of the Nervous Tissue". — Proc. Anat. Soc. Great Britanian and Ireland. 33—38, Taylor & Grancis. London.
QUILLIAM, T. A. (1963): Differences in structure of three lamellated nerve endings. — J. Anat. Lond. *97*, 229.
RICHARDSON, K. C. (1966): Electron-microscopic identification of autonomic nerve endings. — Nature (Lond.) *210*, 756.
SALA, G. (1901): Über den innersten Bau der Herbstschen Körperchen. — Anat. Anz. 595—596.
SAXOD, R. (1968): Ultrastructure des corpuscles sensoriels cutanés de Herbst et Grandry chez le canard. — Arch. Anat. mikr. *57*, 379—400.
SAXOD, R. (1973): Organisation ultrastructurale des corpuscles sensoriels cutanés des oiseaux. — Annales de Centre Universitaire de Savoi, Tome I. Sciences Naturelles. 79—98.
SMITH, C. A. & RASMUSSEN, G. L. (1961): Degeneration in the efferent nerve endings in the cochlea. — J. Ultrastruct. Res. *5*, 184—192.
SMITH, C. A. & SJÖSTRAND, F. S. (1961): A synaptic structure in the hair cells of the guinea pig cochlea. — J. Ultrastruct. Research. *5*, 184—92.
STAMMER, A. (1962): Nerve-endings in the skin of birds. — Acta biol. Hung. *12*, Suppl. *4*, 36.
SCHUMACHER, V. (1911): Beiträge zur Kenntnis des Baues und der Funktion der Lamellen-Körperchen. — Arch. mikr. Anat. *77*, 157—193.
SZYMONOWICZ, L. (1897): Über den Bau und die Entwicklung der Nervenendigungen in Enteschnabel. — Arch. mikr. Anat. *48*, 329—358.

TAMURA, O. (1922): Die Folgen der Nervendurchschneidung am Entenschnabel. — Arch. f. Entwicklungsmech. *51*, 552—574.
TIMOFEJEW, D. (1896): Über eine besondere Art von einkapselten Nervenendigungen in den männlichen Geschlechtsorganen bei Säugetieren. — Anat. Anz. *11*, 44—63.
Van de VELDE, E. (1907): Die fibrilläre Struktur in den Nervenendigungen der Vögel und Säugetiere. — Anat. Anz. *31*, 621—634.
WALTER, P. (1962): Licht- und elektron-mikroskopische Untersuchungen an sensiblen Receptoren von Haustieren. — Anat. Anz. Ergänz. *111*, 198—207.
WERSÄLL, J. (1961): Vestibular receptor cells in fish and mammals. — Acta oto-laryng. Suppl. *163*, 25—62.
WERSÄLL, J. (1956): Studies on the structure and innervation of the sensory epithelium of the cristae ampullares in the guinea pig. — Acta oto-laryng. Suppl. *126*, 1—85.
WILL, J. G. (1850): Vaterschen Körperchen der Vögel, einige Bemerkungen über dieselben. — Sitzungsber. Akad. Wiss. Wien *4*, 213—225.

Address of the author:

Prof. Dr. A. ÁBRAHÁM
Department of Zoology, A. J. University, H-6701 Szeged, P. O. Box 428, Hungary